7. Tundra stream macroalgae of North America: composition, distribution and physiological adaptations

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Abstract

Eighty-three infrageneric taxa of stream macroalgae have been reported from tundra regions of North America, composed of 32 cyanobacteria, 35 Chlorophyta, 10 Chrysophyta and 6 Rhodophyta. There are few if any endemics represented in this flora. The most widespread species are the cyanobacteria *Rivularia minutula*, *Nostoc commune* and *Tolypothrix tenuis* as well as asexual populations of the chlorophyte genus *Zygnema*. The relative contribution of cyanobacteria compared to that of the Chlorophyta increases from the low to high arctic. Number of species per segment ranges from 0 to 7, with a mean of 2.8, and varies little between the low and high arctic. The percentage of stream bottom covered by macroalgae ranges from 0 to ca. 75%; mean cover values for low and high arctic streams are ca. 12 and 8%, respectively. Tundra macroalgae tend to be more abundant and diverse in less rigorously flowing stream sections. Most species tolerate prolonged freezing by forming resistant vegetative cells with thick walls, plentiful reserves and low molecular weight solutes to lower the freezing point. Many tundra stream macroalgae also produce 'sunscreen' pigments to reduce exposure to damaging radiation in the blue and ultraviolet regions. Nutrients tend to be low and phosphorus is often limiting in these systems. Arctic streams appear to differ from those of Antarctica in having potential grazers of macroalgae, such as the chironomid *Diamesa*, the mayfly *Baetis* and the caddisfly *Brachycentrus*.

Introduction

Stream macroalgae can be defined as those species occurring in flowing freshwaters and having a mature thallus which is benthic and a discrete structure recognizable with the naked eye (Sheath & Cole, 1992). Morphological forms include mats, colonies, gelatinous and free filaments, tissue-like thalli, tufts and crusts. These forms possess various adaptive features to tolerate flow-related drag (Sheath & Hambrook, 1990). Arctic species are subjected to additional stresses associated with a shortened growing season during which time the photoperiod is altered to an extended light phase, low nutrients, and potential desiccation prior to a prolonged freezing period (Prescott, 1963).

The arctic tundra occurs above the latitudinal tree-line and comprises about 20% of North America, about 2.5 million km² in Canada, 0.2 million km² in Greenland and 0.3 million km² in Alaska (Bliss, 1988) (Figure 1). It can be divided into the low and high arctic based on a number of environmental characteristics, including length of growing season (3–4 vs. 1.5–2.5 mo), mean July air and soil temperatures at −10 cm (8–12 and 5–8 vs. 3–6 and 2–5°C) and accumulated degree-days above 0°C (600–1400 vs. 150–600) (Bliss, 1988). The low arctic has a more diverse vascular plant flora with woody forms being more common than the high arctic.

This review will examine the hydrology and other characteristics of tundra streams, composition of the macroalgal flora, and some aspects of physiological
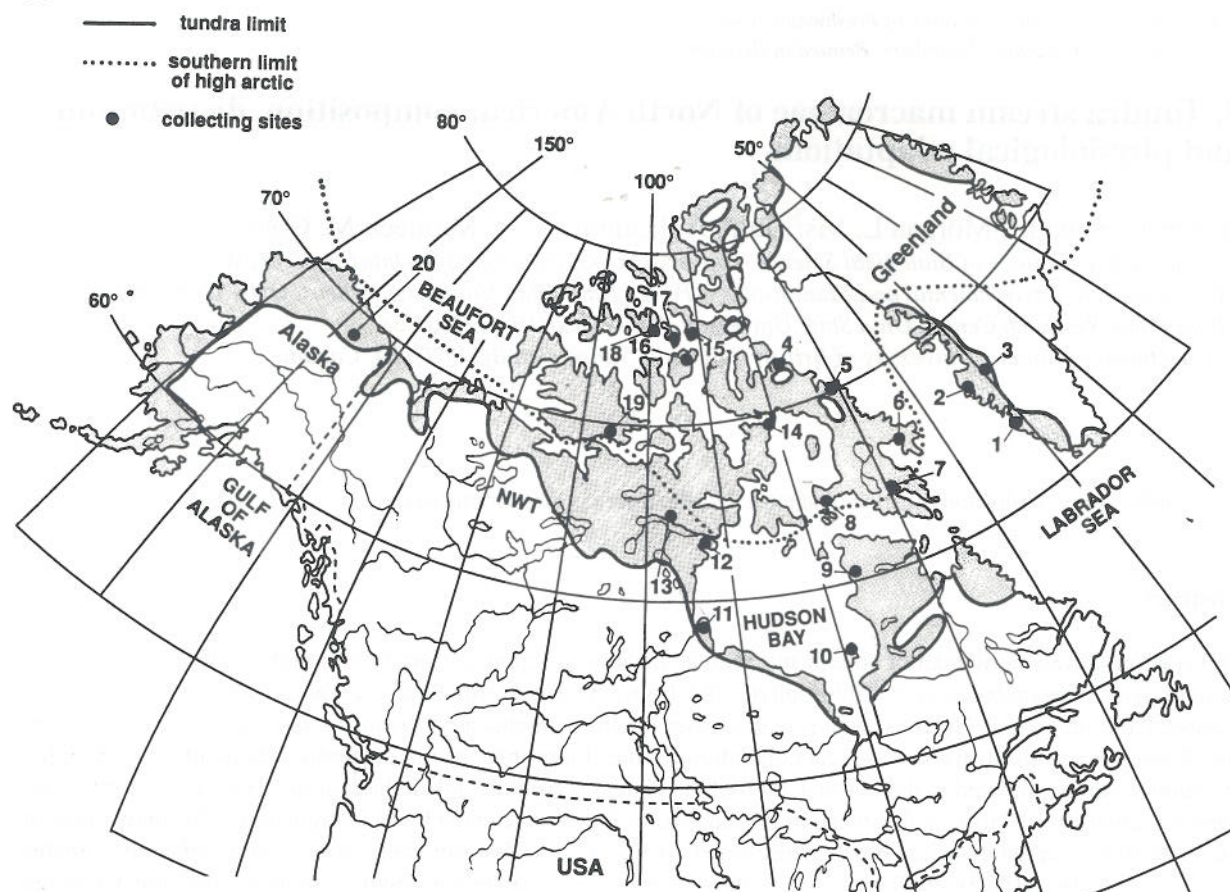
Figure 1. Collecting sites for tundra stream macroalgae of North America, many from the survey of Sheath & Cole (1992). The locations are as follows: 1–3. Greenland. 1. Nuuk, 2. Sisimuit, 3. Kangerlussuaq. 4–8. Baffin Island, N.W.T. 4. Pond Inlet, 5. Clyde River, 6. Pangnirtung, 7. Iqaluit, 8. Cape Dorset. 9. Northern Quebec – Povungnituk. 10. Belcher Islands, N.W.T. – Sanikiluaq. 11. Manitoba – Churchill. 12–13. Keewatin, N.W.T. 12. Rankin Inlet, 13. Baker Lake. 14. Igloolik, N.W.T. 15–18. Queen Elizabeth Islands, N.W.T. 15. Western Devon Island, 16. Cunningham Inlet, Somerset Island, 17. Resolute, Cornwallis Island, 18. Polar Bear Pass, Bathurst Island. 19. Cambridge Bay, Victoria Island, N.W.T. 20. Toolik region, Alaska.

adaptations of arctic species to this harsh environment. The trends will be compared to those of other biomes in North America and stream systems of Antarctica.

Hydrology

There are two basic groups of tundra riverine systems: those that flow solely in the arctic and those that have their origins in the boreal forest biome (Woo, 1991). The majority of stream systems containing macroalgae are of the former type since latter systems are typically quite large and become too deep and turbid to support benthic autotrophs. Most tundra streams have negligible to no flow during the winter, followed by the spring freshet associated with snowmelt (Craig &

McCart, 1975; Rydén, 1977; Woo, 1991). The peak flow may occur in late May to early June in low arctic lowland sites while it often takes place from late June to mid July in many parts of the high arctic (Figure 2). The peak typically extends only two to three weeks but accounts for about 80% of the yearly runoff (Rydén, 1981). This is due to the combined effect of high intensities of solar radiation, a decrease in albedo of snow cover and percolation being greatly reduced by permafrost.

In small streams that are strictly nival (snowmelt dominated) in their hydrology, the channel typically becomes dry after the spring flow except for occasional high rainfalls (Woo, 1991). Glacier-fed streams can have a brief low discharge rate after snowmelt due to cold temperatures and then a second increase
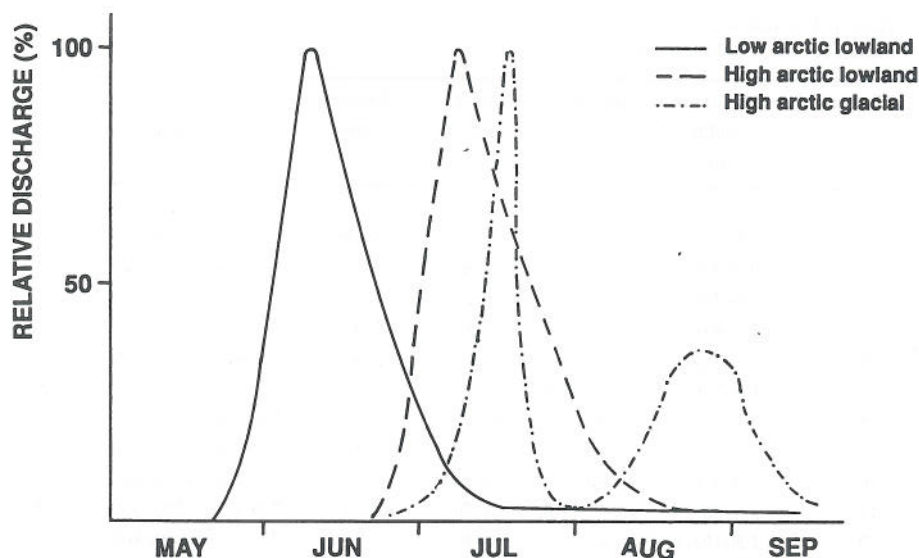
Figure 2. Streamflow regimes of three types of tundra streams based on studies of Craig & McCart (1975), Rydén (1977) and Woo (1991). These regimes typically show additional smaller peaks corresponding to summer rainfall. The base flow after the spring freshet may drop to zero depending on the hydrology of the basin.

from glacier melt (Figure 2). Streams flowing through wetlands have relatively low runoff ratios due to poor drainage and water retention in ponds and peaty soils (Woo, 1988, 1991). Hence, streamflow response to rainfall is attenuated. Lakes also attenuate flow due to water storage. Coastal plain arctic streams often form a series of pools along their course ('beaded streams') and they may have a number of parallel and inter-twining channels ('braided streams') (Harper, 1981). Upland-derived streams tend to have relatively large spring flows which may extend longer than those that are strictly lowland (Figure 2) (Craig & McCart, 1975; Rydén, 1977).

In comparison, antarctic stream discharge appears to be less seasonally predictable with high levels of variability at all time levels (e.g. Vincent et al., 1993b).

Other characteristics of tundra streams

Tundra streams containing macroalgae vary consider-ably in physical and chemical characteristics (Table 1). However, they are typically 1st- to 4th-order reaches which are less than 100 cm in depth and with moderate current velocities. Nival streams tend to be relative-ly turbid during the snowmelt peak whereas glacial streams may be turbid throughout much of the dis-charge period (Milner & Petts, 1994). Tundra streams

tend to be low in nutrients (Moore, 1979; Peterson et al., 1985; Murray & Svoboda, 1989; Peterson et al., 1985, 1993; Hamilton & Edlund, 1994) and levels of nitrogen and phosphorus do not appear to be related to the nature of bedrock drained (Murray & Svoboda, 1989). Phosphorus largely limits algal production in streams examined on the north slope of Alaska and biological processes at all trophic levels are affected by its addition (Peterson et al., 1985, 1993). Phos-phorus limitation in other areas is confirmed by high N:P ratios (e.g. Murray & Svoboda, 1989). However, when tundra streams are phosphorus enriched, nitrogen can become limiting (Hullar & Vestal, 1989). While antarctic streams also tend to have low nutrients, con-centrations of nitrogen and phosphorus range consid-erably with season and time of day associated with freeze-thaw cycles (e.g. Vincent et al., 1993b).

Lowland streams in the low arctic can have high densities of invertebrates ($\bar{x} = 1000 - 22000$ indi-viduals m^{-2}) compared to mountain streams at the same latitudes ($\bar{x} = 293$ individuals m^{-2}) (Craig & McCart, 1975). Common invertebrates in these streams include larvae of the chironomid families Diamesinae and Orthocladinae, the mayfly *Baetis laponicus*, the caddisfly *Brachycentrus americanus* and the black flies *Stegopterna ornata* and *Prosimulium martini* (Slack et al., 1979; Hershey & Hiltner, 1988; Peterson et al., 1993). *Baetis* and *Brachycentrus* potentially graze

Table 1. Physical and chemical characteristics of tundra streams sampled in North America (see Sheath & Cole, 1992 for details)

Location[1]	Maximum width (m)	Maximum depth (cm)	Current velocity (cm s^{-1})	Temperature (°C)	pH	Specific conductance (μS cm^{-1})
1	1.2–3.3	14–35	0–17	7–17	7.1–8.3	20–150
2	0.1–15.0	10– > 100	0–75	4–15	8.0–8.3	10–223
3	0.7–4.0	16–67	1–80	9–13	8.1–8.3	20–90
4	0.9–7.0	15–23	1–59	2–10	–	10–70
5	1.5–8.0	16–160	14–105	2–8	6.6–6.9	0–40
6	0.7–3.0	11–34	8–74	1–3	5.9–6.3	0–10
7	1.0–2.3	15– > 100	1–109	0–9	6.2–7.8	0–20
8	0.8–4.0	12–50	0–72	2–7	6.6–7.8	0–90
9	1.3–5.0	19–60	0–58	9–12	6.6–7.5	20–350
10	0.9–8.3	15–30	8–96	4–11	6.1–8.1	60–440
11	3.5–20.0	46– > 100	10–58	12–17	7.2–8.0	290–630
12	1.3–16.0	15–65	0–40	5–14	7.7–8.3	60–1050
13	1.8–20.0	20–45	15–58	4–16	7.4–8.3	10–250
14	1.9–6.0	9–50	12–86	0–5	8.1–8.9	80–230
15	2.2–20.0	5– > 100	10–127	6–10	8.1–8.9	0–440
16	1.0–20.0	10– > 100	30–56	5–11	8.2–8.3	120–170
17	1.5–12.0	20–56	14–49	3–8	8.0–8.6	110–340
18	5.0–20.0	30– > 100	4–16	6–10	8.4–8.8	120–140
19	2.4–20.0	17–62	34–61	4–10	8.1–8.6	58–500
20	1.5–30.0	11– > 100	0–111	5–15	6.7–8.4	10–300

[1] See Figure 1 for specifics.

macroalgae (Hambrook & Sheath, 1987) and their growth rates increase in response to phosphorus addition (Peterson et al., 1993). Lowland streams in the low arctic are also used as spawning and rearing areas by the grayling (*Thymallus arcticus*) (Craig & McCart, 1975; Peterson et al., 1993). Glacier streams support relatively few benthic invertebrates near the glacier snout and these stretches are often dominated by the chironomid genus *Diamesa* which has been found to graze filamentous algae, such as the cyanobacterium *Phormidium* (Milner & Petts, 1994). Downstream the invertebrate fauna becomes more diverse as channels become more stable. Streams flowing from lakes tend to have high populations of filter feeders (Harper, 1981). Much less is published on the animal communities of high arctic streams. Tributaries of a small lake on Cornwallis Island, N.W.T. are dominated by Chironomidae of *Diamesa* and Orthocladinae (Stockner & Hynes, 1976).

Composition of stream macroalgae

Table 2 is a compilation of macroalgal species from our survey of 150 stream segments from 20 locations (Figure 1) (partly given in Sneath & Cole, 1992) plus ten previous reports from other researchers who clearly indicated that they collected in arctic stream habitats from North America. There have been 83 infrageneric taxa reported, composed of 32 cyanobacteria (39%), 35 Chlorophyta (42%), 10 Chrysophyta (12%) and 6 Rhodophyta (7%). However, 12 of these taxa are not identified to the species level. In addition, some of the identifications may need to be re-examined, such as those of *Prasiola* species (Hamilton & Edlund, 1994). The diversity of this flora is similar to other widely sampled biomes in North America, which have 84 to 100 infrageneric taxa (Sheath & Cole, 1992). Thus, the typical increase in species numbers from the arctic to the tropics that is evident among seaweeds (e.g. Alvarez et al., 1988) is not true of stream macroalgae. However, other riverine organisms also show relatively low difference in diversity with latitude (Patrick, 1988). The majority of the tundra lotic taxa are either

Table 2. Distribution of tundra stream macroalgae in North America

Taxon	Location[1]
Cyanophyta	
Chroococcales	
Aphanothece pallida (Kütz.) Rabh.	11 (L)
Chlorogloea microcystoides Geit.	15, 17 (H)
Gloeocapsa sanguinea (C.Ag.) Kütz.	14, 15 (H)
Tychonema bornetii Anag. & Komár.	18 (H)
Oscillatoriales	
Leptolyngbya tenuis (Gom.) Anag. & Komár.	1, 3, 7 (H,L)
Lyngbya aestuarii (Mert.) Lieb.	17 (H)
Microcoleus sociatus W. & G. S. West	18 (H)
Phormidium autumnale (C.Ag.) Gom.	I, VIII (L)
P. corium (C.Ag.) Gom.	3 (L)
P. retzii (C.Ag.) Gom.	1, 17 (H,L)
P. subfuscum Kütz.	3, 4, 7, 8, 12, 13, 17, 18, 20 (H,L)
P. tenue Gom.	I (L)
P. valderiae (Delp.) Geit.	VIII (L)
P. sp.	VII (L)
Pseudophormidium tenue (Thur. ex Gom.) Anag. & Komár.	14 (H)
Schizothrix calcicola (C.Ag.) Gom.	15, 17, V (H)
S. fuscescens Kütz.	1, 7, 8, 20, VIII (H,L)
S. mexicana Gom.	V (H)
S. muelleri Näg.	1, 19, VI (H,L)
Nostocales	
Nostoc commune Vauch.	1, 2, 4, 7, 8, 9, 10, 12, 13, 14, 15, 17, 18, 19, V (H,L)
N. pruniforme C.Ag.	11, 20 (L)
N. verrucosum Vauch.	14 (H)
N. sp.	I (L)
Rivularia haematites (D.C.) C. Ag.	4, 17, 20, VIII (H,L)
R. minutula (Kütz.) Born. & Flah.	1, 3, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20 (H,L)
Scytonema myochrous (Dillw.) C. Ag.	17 (H)
S. tolypothricoides Kütz.	1, 7, 8, 12, 14 (H,L)
Tolypothrix distorta Kütz.	V, IX (H,L)
T. limbata Thuret	VIII (L)
T. tenuis Kütz. emend. J. Schmidt	1, 2, 8, 9, 10, 12, 13, 15, 17, 18, 19, 20 (H,L)
Stigonematales	
Stigonema mamillosum (Lyng.) C. Ag.	2, 7, 8, 14, 20, VI, VIII, IX (H,L)
S. ocellatum (Dillw.) Thuret	8 (H)
Chlorophyta	
Tetrasporales	
Tetraspora sp.	I (L)
Ulotrichales	
Cylindrocapsa conferta W. West	6 (H)
Hormidiopsis ellipsoideum Presc.	7 (H)
Microspora elegans Hansg.	1, 2, 12, 20 (L)
M. loefgrenii (Nordst.) Lagerh.	6, 7, 11 (H,L)

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Taxon	Location[1]
M. tumidula Hazen	2, 3, 4, 6, 7, 9, 12, 14, 20, V (H,L)
M. sp.	I, III (L)
Ulothrix aequalis Kütz.	IX (L)
U. tenerrima Kütz.	17 (H)
U. tenuissima Kütz.	13, 20 (L)
U. variabilis Kütz.	11, 16, 17 (H,L)
U. zonata (Weber & Mohr) Kütz.	17, VIII (H,L)
Chaetophorales	
Chaetophora elegans (Roth) C. Ag.	20 (L)
C. incrassata (Huds.) Hazen	9, 10 (L)
Draparnaldia glomerata (Vauch.) C. Ag.	20 (L)
D. mutabilis (Roth) Cedergren	11 (L)
D. sp.	III (L)
Stigeoclonium flagelliferum Kütz.	20 (L)
S. nanum Kütz.	13 (L)
S. subsecundum Kütz.	7 (H)
Dichotomosiphonales	
Dichtomosiphon tuberosus (Braun) Ernst	14 (H)
Oedogoniales	
Bulbochaete sp.	20 (L)
Oedogonium spp.	2, 7, 8, 18, 20, IX (H,L)
Cladophorales	
Rhizoclonium hieroglyphicum (C.Ag.) Kütz.	10, 19 (H,L)
R. hookeri Kütz.	11 (L)
Prasiolales	
Prasiola fluviatilis (Sommerf.) Aresch.	V, X (H)
P. mexicana J. Ag.	2, 12 (L)
Zygnematales	
Cylindiocystis brebissonii var. brebissonii Croads.	1, 14 (H,L)
Mougeotia spp.	10, VI, IX (H,L)
Mougeotiopsis calospora Palla	4 (H)
Spirogyra groenlandica Rosenvinge	2, 4, I (H,L)
S. inflata (Vauch.) Kütz.	III (L)
S. spp.	1, 18, 20, I (H,L)
Zygnema insigne (Hassall) Kütz.	12 (L)
Z. spp.	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 14, 15, 17, 18, 19, 20, I, III, VII, IX (H,L)
Chrysophyta	
Chromulinales	
Hydrurus foetidus (Vill.) Trev.	20, I, IX (L)
Tribonematales	
Tribonema affine (G. S. West) G. S. West	V (H)
T. utriculosum (Kütz.) Hazen	14 (H)
T. viride Pasch.	12 (L)
T. sp.	I (L)
Fragilariales	
Tabellaria flocculosa (Roth) Kütz.	1, 2, 3, 9 (L)

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| Taxon	Location[1]
Meridion circulare (Grev.) C. Ag.	16, VII (H)
Naviculales	
Cymbella cistula (Ehr.) Kirchn.	17, 18 (H)
C. prostrara (Berk.) Cl.	11 (L)
Didymosphenia geminata (Lyngb.) M. Schmidt	20 (L)
Rhodophyta	
Acrochaetiales	
Audouinella hermannii (Roth) Duby	20 (L)
Batrachospermales	
Batrachospermum gelatinosum (L.) DC.	4, 6, 7, 8, 9, 11, 20 (H,L)
B. skujae Geitler	1 (L)
B. spermatoinvolucrum Vis & Sheath	1, 3, 4, 5, 6, 7, 13, 20 (H,L)
B. sp.	1, 3, 6, 10, 11, 19, 20, I (H,L)
Lemanea borealis Atk.	3, 20 (L)

[1] 1–20 stream locations from our survey (see Figure 1); I – Bachmann (1921) – West Greenland; II – Petersen (1924) – north coast of Greenland; III – Yamagishi (1967) – Beaufort Sea coast of Alaska; IV – Kobayashi (1967) – Beaufort Sea coast of Alaska; V – Croasdale (1973) – Lake Hazen, Ellesmere Island, N.W.T.; VI – Moore (1974) – southern Baffin Island, N.W.T.; VII – Stockner & Hynes (1976) – Cornwallis Island, N.W.T.; VIII – Moore (1979) – Beaufort Sea drainage area of N.W.T.; IX – Johansson (1980) – Narssaq area, south Greenland; X – Hamilton & Edlund (1994) – northern Ellesmere Island, N.W.T.; H = high arctic; L = low arctic.

mat-forming filaments (59%) or colonial forms (22%). Antarctic streams also are predominated by cyanobacteria and green algae, many of which are in mats or colonies (Broady, 1982; Vincent & Howard-Williams, 1986; Hawes, 1989; Davey & Clarke, 1992; Vincent et al., 1993a). In antarctic streams, green algae have their greatest abundance in the maritime zone while cyanobacteria typically dominate streams on the Antarctic continent (Vincent et al., 1993b). It is noteworthy that Rhodophyta have not been collected in antarctic streams, whereas they are common in the arctic.

The most widespread species in our survey of 20 arctic locations were the cyanobacteria: *Rivularia minutula* (15), *Nostoc commune* (13) and *Tolypothrix tenuis* (12) (Table 2). In addition, asexual populations of the chlorophyte genus *Zygnema* were present in all but two locations. Some of the widely distributed species are presented in Figures 3–17. *Nostoc commune* and *Zygnema* spp. are also common in antarctic streams (Hawes, 1989; Vincent et al., 1993a).

Of the 83 infrageneric taxa in tundra streams of North America, 34 were found only in the low arctic, 22 only in the high arctic and 27 were collected in both regions (Table 2). The proportion of cyanobacteria and Chlorophyta is largely reversed between the low arctic (34 and 46%, respectively) and high arctic (48 and 38%, respectively). At least 21% of the high arctic taxa are capable of nitrogen fixation, based on the presence of heterocysts, but additional species of cyanobacteria probably undergo this process (e.g. Pandey et al., 1992).
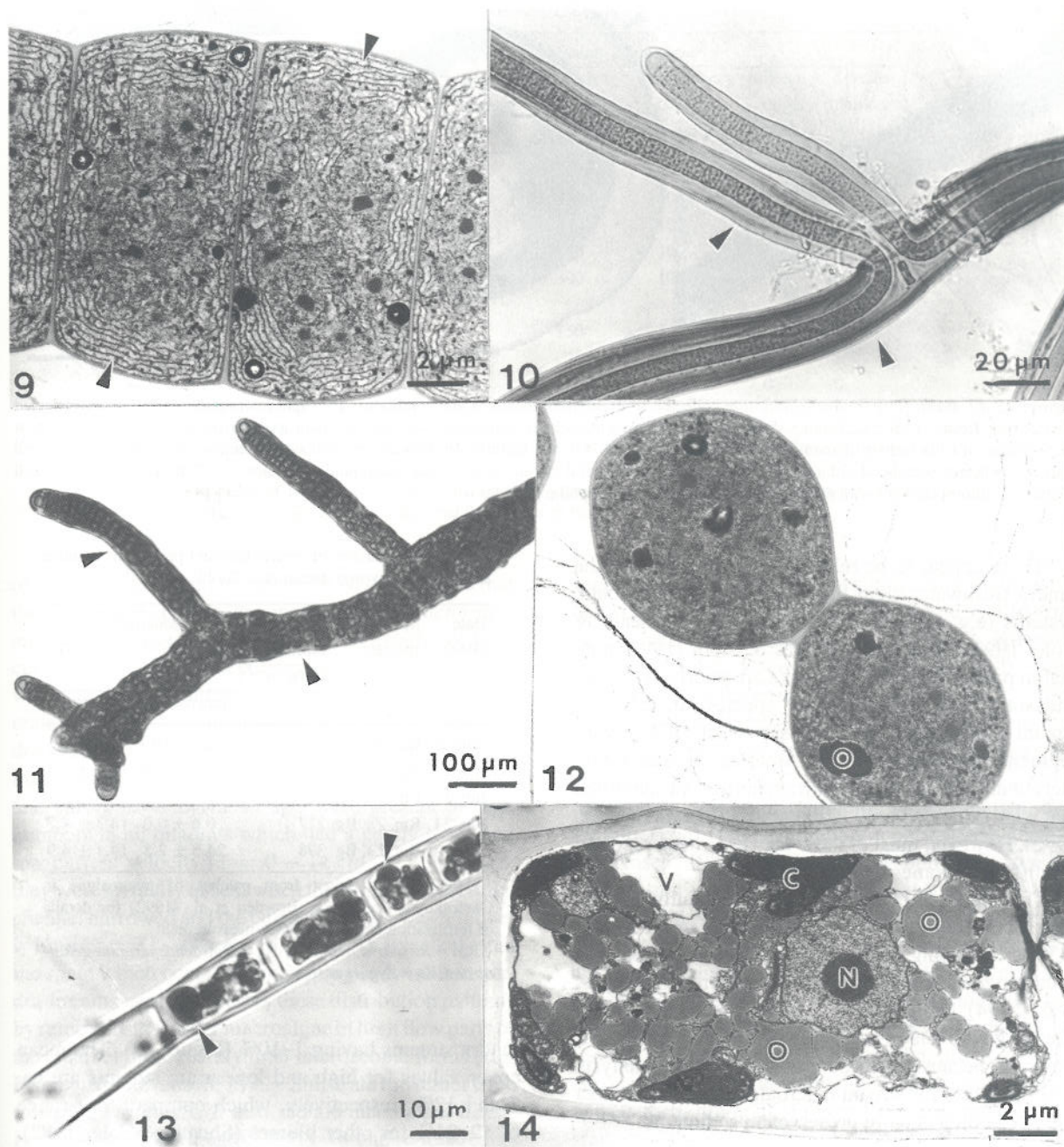
The number of species per stream segment (minimum area examined 100 m^2) in our survey of tundra streams varies from zero to seven with a mean of 2.8 (Figure 18). The high arctic streams tend to have a slightly lower number (most frequently two per segment, $\bar{x} = 2.7$) than those of the low arctic (most frequently three per segment, $\bar{x} = 2.9$). These numbers compare to mean numbers of 2.9–3.6 per stream segment in other biomes in North America (Sheath & Cole, 1992).
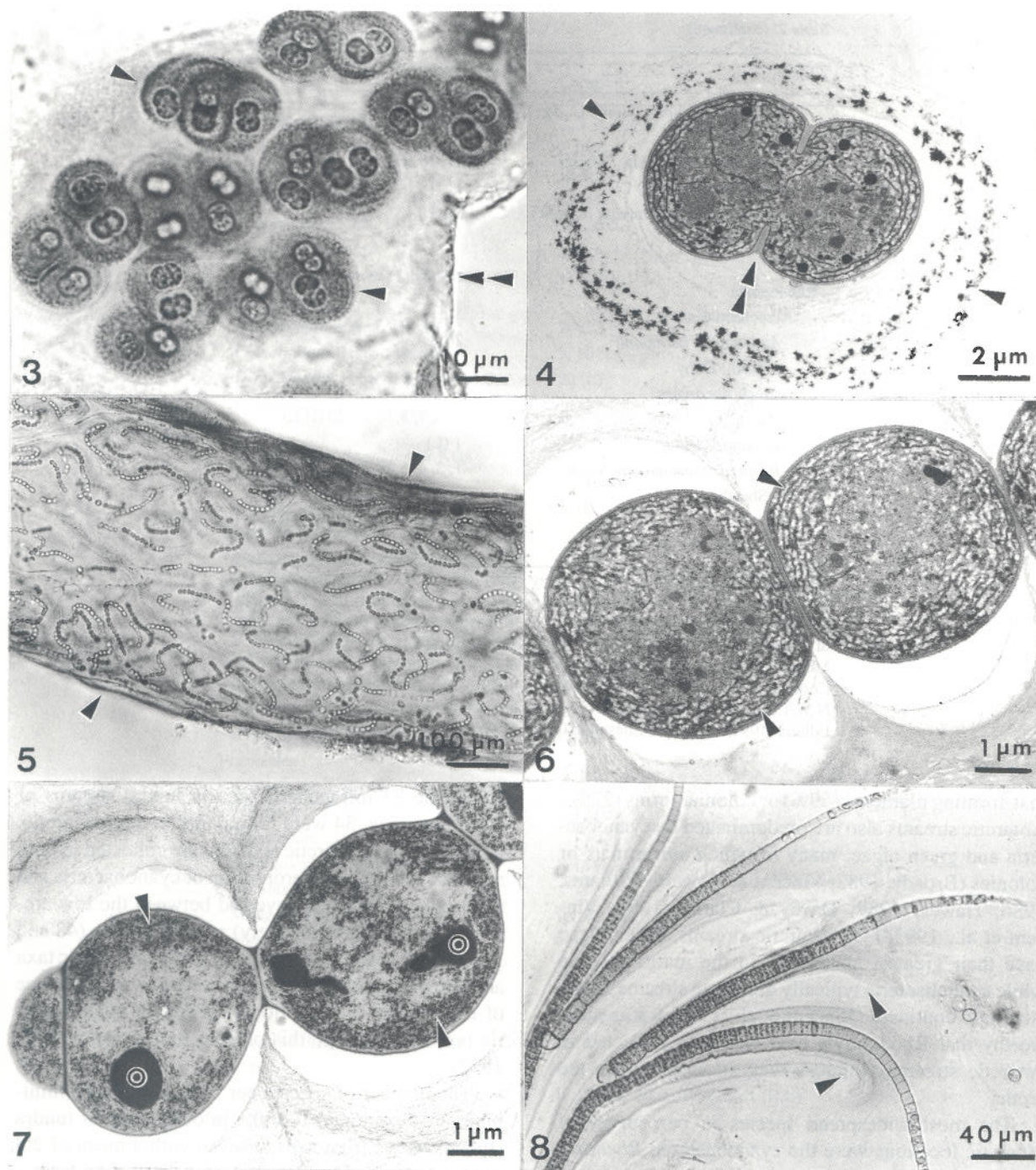
Figures 3–8. Common tundra stream cyanobacteria: 3–4 *Gloeocapsa sanguinea* collected at snowmelt from Igloolik, N.W.T. (81): 3. Light micrograph showing crimson-colored sheath surrounding small packets of cells (single arrowheads) all enclosed in a common colorless colonial sheath (double arrowhead). 4. Electron micrograph showing granulate, layered sheath (single arrowheads) surrounding a cell undergoing division (double arrowhead). The peripheral thylakoids surround the central cytoplasm which has several, small electron dense globules. 3–7. *Nostoc commune* from various locations and conditions: 5. Light micrograph of a cross-section of a colony showing brown-colored, leathery sheath (arrowheads) enclosing many filaments (N.W.T. 83 – Igloolik at snowmelt). 6. Electron micrograph of two cells fixed at the time of snowmelt (N.W.T. 81, Igloolik) with typical cell structure, including concentric, peripheral thylakoids (arrowheads) and small, electron-dense globules. 7. Electron micrograph of two cells from a highly desiccated colony collected over one month after the spring freshet (N.W.T. 97, Bathurst Island). The peripheral thylakoids are not as obvious (arrowheads), the central cytoplasm is less granular and large osmiophilic granules (O) are present in each cell. 8. *Rivularia minutula* collected at snowmelt at Igloolik, N.W.T. (84). Light micrograph showing tapering filaments surrounded by lamellated, brownish, flared sheath (arrowheads).

Figures 9–14. Common cyanobacteria (9–12) and Tribophyceae (13–14) from tundra streams: 9. *Rivularia minutula* collected at snowmelt from Igloolik, N.W.T. (84). Electron micrograph of two cells with typical concentric, peripheral thylakoids (arrowheads) and numerous, small, osmiophilic globules. 10. *Scytonema tolypothricoides* collected at snowmelt from Igloolik, N.W.T. (85). Light micrograph showing the lamellated sheath which is yellow-to brown-colored (arrowheads). 11–12. *Stigonema mamillosum* collected from different locations: 11. Light micrograph of multiseriate filament with brown-colored sheath collected after spring freshet (GLD 10). 12. Electron micrograph of two cells from a filament collected at snowmelt (N.W.T. 86, Igloolik) with typical cell structure and large, osmiophilic globules in most cells (O). 13–14. *Tribonema utriculosum* collected and fixed while still frozen at the time of snowmelt (N.W.T. 83, Igloolik): 13. Light micrograph of a filament stained with sudan Black B, showing positively-stained lipid bodies (arrowheads). 14. Electron micrograph of a longitudinal section through a cell with many osmiophilic globules (o), small vacuoles (v), a central nucleus (n), and peripheral chloroplasts (c).
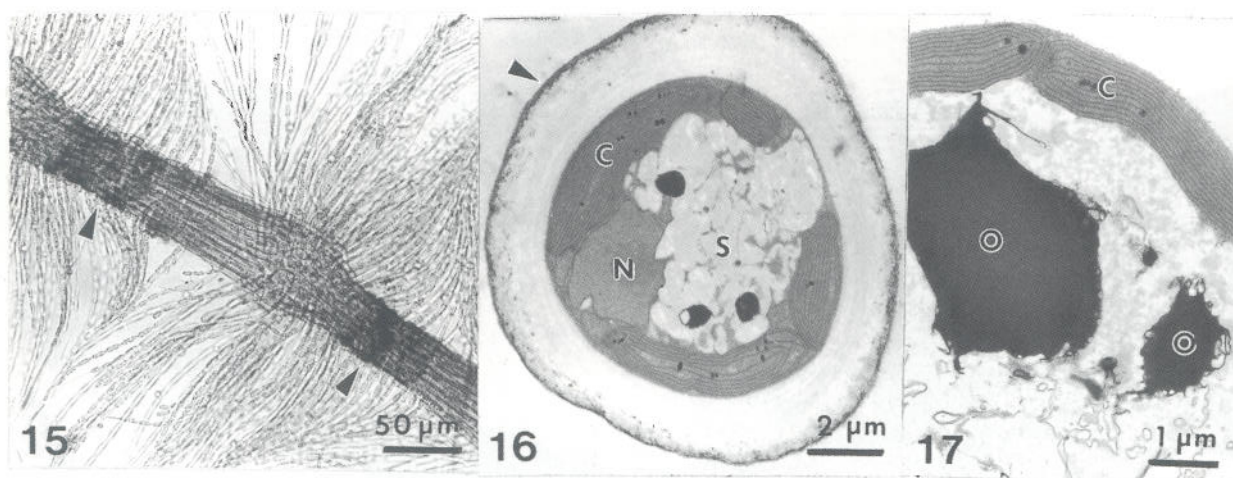
Figures 15–17. *Batrachospermum gelatinosum* collected from different locations and conditions: 15. Light micrograph of a filament collected after spring freshet (AK 58, Toolik) showing orange-brown-pigmented cortication surrounding main axis (arrowheads). 16–17. Electron micrographs of cells from a filament collected at snowmelt (N.W.T. 90, Iqaluit). 16. Fascicle cell transverse section, showing very thick cell wall (arrowhead), peripheral chloroplasts (c), nucleus (n), plentiful starch (s) and some osmiophilic globules. 17. Periphery of fascicle cell containing chloroplasts (c) with intact thylakoids and large osmiophilic globules (o).

There appear to be relatively few endemics in the tundra freshwater algal flora, either in lotic or lentic systems (e.g. Sheath & Steinman, 1982; Sheath & Cole, 1992). However, Douglas & Smol (1993) note that in parts of the arctic, the taxa are poorly described and some may represent new species. In terms of stream macroalgae, from our survey of 1000 stream segments throughout North America, it was found there were 13 out of 259 infrageneric taxa identified that were collected only in the tundra (Sheath & Cole, 1992). However, most of these taxa have been reported for different biomes by other researchers.

The diatom flora has changed significantly in some high arctic ponds on Cape Herschel, Ellesmere Island, N.W.T. beginning in the 19th century in response to anthropogenic impacts on the environment (Douglas et al., 1994). Douglas et al. (1994) propose that it may already be too late to catalogue natural assemblages in the arctic because of these changes. Such an analysis is not possible for stream macroalgae since most taxa are soft-bodied and not preserved in sediments.

Effects of environmental factors and physiological adaptations

As in other biomes, the distribution of tundra stream macroalgae is quite variable within and among streams. The percentage of stream bottom covered by macroalgae varies from 0 to ca. 75% with the majority of

Table 3. Comparison of macroalgal and periphytic biomass and productivity in a stream near Toolik, Alaska[1]

Date (1990)	Macroalgal species[2]	Macroalgal biomass (g fw m^{-2})	Net productivity (mg O_2 h^{-1} m^{-2} ± SE)	
			macroalgae	periphyton
June 22	Rm, Bg	558	35.8 ± 10.1	8.0 ± 2.6
	Rm	68	0.7 ± 0.4	10.6 ± 5.5
July 10	Rm, Bg	897	60.9 ± 4.7	16.8 ± 3.1
July 23	Rm, Zs, Bg	217	0.6 ± 0.0	14.3 ± 4.7
	Rm, Zs, Bg	398	24.5 ± 2.3	14.1 ± 4.9

[1] Measurements taken from patches of macroalgae in Okstrukuyik Creek. See Bowden et al. (1992) for details of fertilization and productivity measurement.
[2] Rm = *Rivularia minutula*, Bg = *Batrachospermum gelatinosum*, Zs = *Zygnema* sp.

tundra streams having 1–10% (Figure 19). The mean cover values for high and low arctic streams are ca. 8 and 12%, respectively, which compare to a range of 12–21% for other biomes (Sheath & Cole, 1992). Even within patches of macroalgae, the biomass and net productivity vary considerably in the same stream (Table 3). In addition, the contribution to total net productivity by macroalgae can range from ca. 4 to 82%.

Streams are often considered to be physically controlled environments in which flooding, droughts and rapid temperature changes can act as major sources of density-independent mortality (Hart, 1983). This is particularly true of tundra streams. In a mapping study

Table 4. Effect of stream slope on macroalgal abundance in a high arctic stream at Resolute, N.W.T. (NWT 104)

Distance from source[1] (m)	Slope (cm/m)	Channel width (m)	Mean current velocity (cm s^{-1})	Stream macroalgae[2]			
				Mean Number of entities	Frequency (% of quadrats)	Mean cover (%)	Species number
1. Gradual slope region:							
0	9	24.5	10	440	100	5	3
60	9	14.0	15	330	100	1	2
180	11	14.5	13	540	100	3	2
420	11	17.5	14	300	100	0.9	3
2. Steep slope region:							
540	18	5.0	41	150	100	0.2	2
600	18	4.0	48	20	25	0.1	1
720	18	7.0	37	0	0	0	0
960	22	1.2	64	0	0	0	0

[1] Mapped in m^2 quadrats across the stream segment at these distances from the outflow of a tundra pond.

[2] In order of frequency: *Rivularia minutula*, *Zygnema* sp., *Scytonema myochrous* and *Nostoc commune*; entities are either discernable colonies or mats.

of a high arctic stream in Iqaluit, N.W.T., we found that the domninant species, the rhodophyte *Batrachospermum gelatinosum*, was essentially an avoider of high current velocities by occurring only along the banks where the substratum is stable and the flow is moderate (Figure 20). Similarly, in a relatively large tundra stream in Resolute, N.W.T., the two predominant macroalgae, the cyanobacterium *Rivularia minutula* and chlorophyte *Zygnema* sp., were present in high numbers in all quadrats which had a gently slope and low current velocity ($\bar{x} = 0 - 14$ cm s^{-1}). However, they were virtually absent when the slope increased, the channel narrowed and the current velocity was relatively high ($\bar{x} = 37 - 64$ cm s^{-1}) (Table 4). It is likely that the spate which occurs during spring snowmelt in tundra streams partially creates these distribution patterns by removing the larger macroalgae in high flow parts of the channel more readily than microscopic forms (e.g. Peterson & Stevenson, 1992). Substrata movement due to strong currents will also reduce macroalgal density (Hambrook & Sheath, 1991). In antarctic streams expanded sheets of *Prasiola* (Broady, 1989) and mats of *Zygnema* (Hawes, 1989) are also restricted to less rigorous flowing regions.

The fact that so many taxa tolerate an eight-to ten-month period of freezing is somewhat surprising because few tundra species undergo sexual reproduction to form a resistant spore for over-wintering (Prescott, 1963; Sheath & Steinman, 1982). Hence,

vegetative cells must be physiologically adapted to withstand prolonged freezing. This trend is also true of antarctic stream macroalgae (Vincent & Howard-Williams, 1986; Davey, 1989; Hawes, 1990). The common cyanobacteria species have a thick extracellular mucilaginous layer and an accumulation of reserve products within the cytoplasm, but otherwise the over-wintering cell is typical (Figures 3–12). The reserve products are osmiophilic, indicating that they are either cyanophycin granules or polyphosphate bodies (Jensen, 1985). While the chrysophyte *Tribonema utriculosum* is still encased in ice at the end of winter it has thick walls, plentiful lipid globules, numerous small vacuoles, but the nuclei and chloroplasts are in good shape (Figures 13–14). At snowmelt the rhodophyte *Batrachospermum gelatinosum* also has very thick walls (up to 2 μm thick) and the major reserve product is floridean starch (Figure 16). There are some osmiophilic globules in these cells which appear to be lipoidal (Figure 17) based on previous studies of this genus (Sheath & Whittick, 1995). The common condition among all of these algae in the over-wintering state, a thick extracellular covering and plentiful reserve products, is typical of many algae under prolonged stress (Morison & Sheath, 1985). The ability of these resistant vegetative cells to survive the long winter is due to prevention of intracellular ice crystallization (Hawes, 1990). Crystallization of water inside the cell may occur by internal nucleation or by penetra-
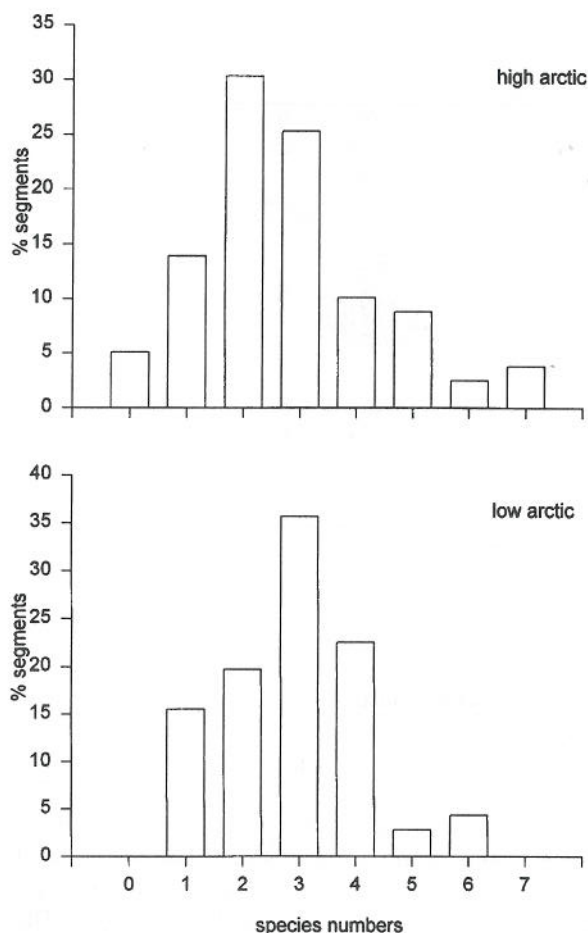
Figure 18. Diversity of stream macroalgae in high arctic ($n = 79$) and low arctic stream segments ($n = 71$) from our survey of 150 segments from 20 locations (see Figure 1).

Figure 19. Frequency of cover values in each stream segment from the high arctic ($n = 79$) and low arctic ($n = 71$).

tion into the cell by external ice crystals (Guy, 1990). Many algae produce low-molecular solutes to lower the freezing point, thereby functioning as cryoprotectants. In addition, restructuring of lipid components in membranes is likely. These phenomena are in turn affected by rate of freezing, number of freeze-thaw cycles, prevailing light conditions and amount of available free water (Davey, 1989; Hawes, 1990). The chrysophyte *Tribonema viride*, collected at Igloolik, N.W.T., exhibits a slight but significantly greater frequency of cell viability after freezing if the cells are previously partially desiccated (Table 5). Cyanobacterial mats in antarctic meltwater streams retain a high metabolic capacity while they are dry and frozen and they respond rapidly to rehydration (Vincent & Howard-Williams, 1986). Nonetheless, severe desiccation causes some
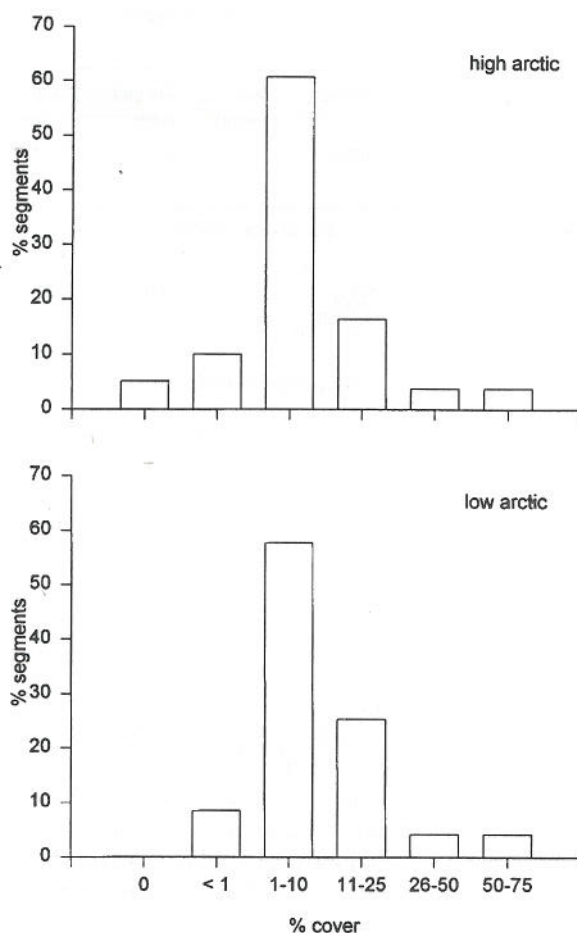
cellular disruption in *Nostoc commune* collected on Bathurst Island, N.W.T. (Figure 7).

Pools may act as refugia for macroalgae in 'beaded' arctic streams because they retain their water much longer after snowmelt than shallow riverine channels. In our survey of 150 tundra streams, pools constituted the most common habitat of certain taxa, such as species of *Microspora* and *Batrachospermum* (Sheath et al., unpubl.). It may be that a more gradual desiccation allows sufficient time for these taxa to produce cryoprotectant compounds that can be used for tolerance of both drying and freezing (Morison & Sheath, 1985). Distribution of filamentous green algae in streams of Signy Island, Antarctica is also related to depth (Hawes, 1989).

Photoperiod affects tundra stream macroalgae in a variety of ways. The paucity of resting spores among

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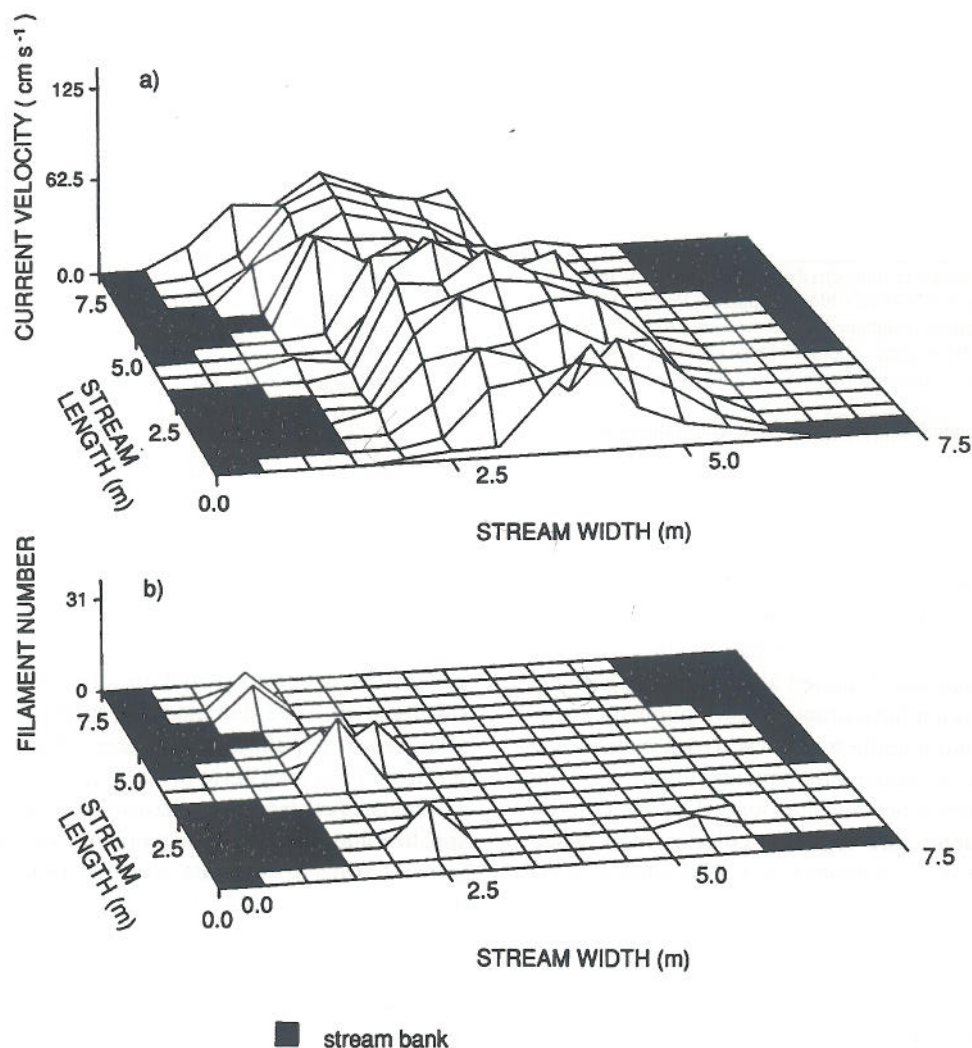high exp
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Figure 20. Distribution of the dominant macroalga, *Batrachospermum gelatinosum*, in relation to current velocity within a mid-sized stream segment in Iqaluit, N.W.T. The stream was mapped in 0.25 m² quadrats in which current velocity and filament number were determined on July 2–3, 1988 (near the end of spring freshet).

these species is partly due to a lack of diurnal light-dark alternation during the growing season which prevents those taxa requiring daylength induction from undergoing sporulation or gametogenesis (Prescott, 1963; Sheath & Steinman, 1982). This situation contrasts with ecotypes of arctic vascular plants which have physiological responses to daylengths greater than 20 hours (Vankat, 1979).

The long photoperiod also results in potentially high exposure to damaging radiation in the blue and ultraviolet regions (Stonehouse, 1989). This is compounded by a recent rise in ultraviolet-B flux in parts of the North American arctic due to ozone depletion

(Vincent & Roy, 1993). A number of tundra macroalgae produce 'sunscreen' pigments to filter out these wavelengths. The cyanobacteria frequently have dark-colored sheaths, such as the crimson one of *Gloeocapsa sanguinea* (Figures 3–4) or the yellowish to brown-colored ones of *Rivularia minutula* (Figure 8), *Scytonema tolypothricoides* (Figure 10), and *Stigonema mamillosum* (Figure 11). The reddish color has been ascribed to gloeocapsin and the yellow-brown color to scytonemin (Whitton, 1992). Antarctic cyanobacterial mats also are enriched with scytonemin (Vincent et al., 1991a). Scytonemin is not unique to polar cyanobacteria but is common to more than 30 species

Table 5. Viability counts of *Tribonema viride* (Tribophyceae, Chrysophyta) collected from Igloolik, N.W.T. and subjected to different moisture and temperature treatments in culture (number of live cells per 100 cells)

Temperature treatment	Moisture treatment	
	BBM (control)	BBM (desiccated)
10°C (control)	97.5 ± 1.3[1]	88.0 ± 1.6[2]
−15°	89.0 ± 1.9[3]	98.3 ± 2.4[1,2]

[1] Values are means of four petri dishes ± SD. Viability determined using 0.05% Evan's blue (Crippen & Perrier, 1974). Moisture regimes maintained for 28 days prior to subjecting them to the temperature conditions for an additional 28 days.
[2] Denotes a significant difference from moisture control at $P < 0.05$.
[3] Denotes a significant difference from temperature control at $P < 0.05$.

Table 6. Frequency of orange-brown cortication surrounding main axis in *Batrachospermum gelatinosum* (Batrachospermales, Rhodophyta) from different biomes of North America

Biome	Frequency of orange-brown cortication (%)	Sample size
tundra	67	15
boreal forest	50	14
western coniferous forest	29	7
hemlock hardwood forest	21	14
deciduous forest	17	12
coastal plain	20	7

which have been exposed to intense solar radiation (Garcia-Pichel & Castenholz, 1991). The pigment is lipid soluble and has a prominent absorption maximum in the near ultraviolet range of the spectrum. Tundra populations of the red alga *Batrachospermum gelatinosum* often have orange-brown pigmented cortication surrounding the main axis which may be due to an increase in carotenoid pigments (Figure 15). The axial cells, which become surrounded by the colored cortical filaments, are typically colorless and hence they do not have carotenoids to act as an internal 'sunscreen' for protection of nucleic acids. Colored cortication is not unique to tundra populations of *Batrachospermum gelatinosum* but its incidence is considerably higher in the arctic compared to that for other biomes in which this taxon occurs (67 vs 17–50%, respectively) (Table 6). A second advantage to having dark pigmentation in the outer layers of thalli of many tundra stream macroalgae is a slight but possibly important rise in thallus temperature (Hebert & McWalter, 1983). This increase in temperature may allow them to complete the life history within the cold waters and short growing season. Arctic species probably employ other mechanisms for UV-protection noted by Vincent & Roy (1993), including production of mycosporine-like amino acids for additional 'sunscreening', quenching of toxic products of UV and oxygen with carotenoid pigments and superoxide dismutase, and efficient DNA repair mechanisms.

The typically low concentrations of nutrients present during the brief growing season are an additional source of potential limitation to the production of tundra stream macroalgae. For example, when the Kuparuk River on the north slope of Alaska is fertilized with phosphate and ammonium, epilithic chlorophyll *a* and photosynthetic rates are greatly increased, particularly in pools (Bowden et al., 1992). Much of this production is due to periphytic diatom communities (Miller et al., 1992) but macroalgae are also enhanced (Hambrook, unpubl.). When these tundra streams are fertilized for a long period (seven years) certain mosses, such as *Fontinalis neomexicana* and *Hygrohypnum* spp. become abundant (Bowden et al., 1994), and compete for suitable substrata with macroalgae. In contrast, nutrient enrichment experiments on glacier-fed ephemeral streams of southern Victoria Land, Antarctica, do not support the concept of N or P limitation to pigment content or photosynthetic rates of cyanobacterial mats (Howard-Williams & Vincent, 1989).

Little has been published on grazing of tundra stream macroalgae or other trophic dynamics involving these taxa. Hawes (1989) noted that herbivory of green algal mats in streams on Signy Island, Antarctica was nil due to the absence of invertebrate grazers. Rather, sloughing was the major mechanism of biomass reduction. Thus, the presence of potential grazers in arctic streams, as noted previously, is one key difference from those of Antarctica.

Conclusions

The tundra stream macroalgal flora at North America constitutes a northern extension of a portion of the temperate community rather than an assemblage of unique species. These taxa appear to be well adapted to this harsh environment by producing resistant vege-

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tative cells for over-wintering, 'sunscreen' pigments to reduce high energy ultra-violet and blue radiation and the ability to grow in a short period of time at low temperatures and nutrients. It is clear that there is much to study before we fully understand the biology of stream macroalgae of the tundra. Because few of these taxa are endemic to the arctic, molecular studies comparing tundra populations with those from other biomes and other polar regions would be useful in determining biogeographic patterns. Biochemical mechanisms of cellular cryoprotection should be examined in terms of the types of low molecular solutes formed for freezing point depression. Population dynamics of recruitment, growth, reproduction and dispersal would be useful to study. In addition, trophic dynamics of tundra stream macroalgae should be related to epilithic periphyton and to localized physical factors.

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